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A Spatial Perspective on the Phenological Distribution of the Spring Woodland Caterpillar Peak

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ABSTRACT: A classic system for studying trophic mismatch focuses on the timing of the spring caterpillar peak in relation to the breeding time and productivity of woodland passerine birds. Most work has been conducted in single-site oak woodlands, and little is known about how insights generalize to other woodland types or across space. Here we present the results of a 3-year study on the species composition and temporal distribution of the spring caterpillar peak on different tree taxa across 40 woodland sites spanning 2° of latitude in Scotland. We used molecular barcoding to identify 62 caterpillar species, with winter moth (*Operophtera brumata*) being the most abundant, comprising one-third of the sample. Oak (*Quercus* sp.) and willow (*Salix* sp.) hosted significantly higher caterpillar abundances than other tree taxa, with winter moth exhibiting similar trends and invariably proportionate across tree taxa. Caterpillar peak phenology was broadly similar between tree taxa. While latitude had little effect, increasing elevation increased the height of the caterpillar peak and retarded timing by 3.7 days per 100 m. These findings extend our understanding of how mismatch may play out spatially, with caterpillar peak date varying with elevation and tree taxa varying in the caterpillar resource that they host.

Keywords: host tree species, Lepidoptera caterpillars, oak *Quercus*, phenology, trophic mismatch, winter moth *Operophtera brumata*.

Introduction

Trophic mismatches—where asynchrony between a consumer and an ephemeral resource negatively impacts the consumer's fitness—have received much research attention (Durant et al. 2007; Forrest and Miller-Rushing 2010). One of the most popular study systems is the deciduous tree–

caterpillar–insectivorous passerine bird food chain in temperate deciduous woodlands (Visser et al. 1998; Both et al. 2006; Charmantier et al. 2008). At the center of this food chain is the ephemeral annual spring caterpillar peak, which varies in height (i.e., abundance/biomass) and timing from year to year (Southwood et al. 2004; Forkner et al. 2008). In deciduous woodlands, this peak coincides with the timing of newly emerged leaves before they become tanninized and less palatable (Feeny 1970; van Asch and Visser 2007). Breeding in synchrony with this peak is of vital importance for the productivity of some passerine birds, such as certain tit (*Paridae*) and flycatcher (*Ficedula*) species (Both et al. 2004; Visser et al. 2006; Burger et al. 2012).

Despite its central position, the caterpillar peak is the least well understood component of this food chain, with its timing and abundance having been predominantly studied indirectly through frass fall (fecal matter; Visser et al. 1998; Smith et al. 2011) or half-fall (intercepting fully grown caterpillars of certain species falling to earth to pupate; Charmantier et al. 2008; Hinks et al. 2015) and usually in the context of oak-dominated (*Quercus* sp.) woodlands (Charmantier et al. 2008; Smith et al. 2011; Burgess et al. 2018). These standard methods for monitoring caterpillar biomass have limitations, with frass not revealing caterpillar species composition or the contribution made by other invertebrates and half-fall capturing only the full-grown larvae of species that descend to ground level, which may not correlate perfectly with the arboreal abundance of earlier life stages of these species or caterpillars of other species that do not descend.

Temperate deciduous woodlands comprise many different tree species across wide latitudinal and elevational gradients, and the passerine birds studied as part of this food chain typically forage and nest in a variety of woodland types (Perrins 1979; Blair and Hagemeijer 1997). To understand whether this induces spatial variation in phenological mismatch, we first need to gain insight into how the temporal distribution of caterpillars varies spatially and on tree species

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other than oak. Several aspects of the seasonal caterpillar peak could vary, including the height (peak biomass), timing of the peak date (phenology), and breadth (duration) of the peak (fig. 1A). In locations or years when mismatch between the timing of peak avian demand and the timing of the oak caterpillar peak is pronounced, deleterious effects on avian productivity could be buffered locally by a differing caterpillar peak timing on other tree species providing alternative resources (Burger et al. 2012; fig. 1B; tree species buffering hypothesis) or at the landscape scale by better matched caterpillar peaks at other locations (fig. 1D; landscape buffering hypothesis). Alternatively, a degree of buffering might arise if some caterpillar species (fig. 1C; dietary

buffering hypothesis) or habitats provide a resource that is available for a longer duration.

In temperate deciduous woodlands, the spring caterpillar peak is often dominated by one or two abundant species (Hunter 1992; Butler and Strazanac 2000; Wesolowski and Rowinski 2006), such as winter moth (*Operophtera brumata*) in Europe (Hunter 1992; Wesolowski and Rowinski 2006). The winter moth is a trophic generalist feeding on a broad range of tree and shrub species (Kerslake and Hartley 1997; Wesolowski and Rowinski 2006; Waring and Townsend 2017) and a major dietary component for small woodland passerines, especially for nestlings (Visser et al. 1998; Wilkin et al. 2009; Cholewa and Wesolowski 2011). Close

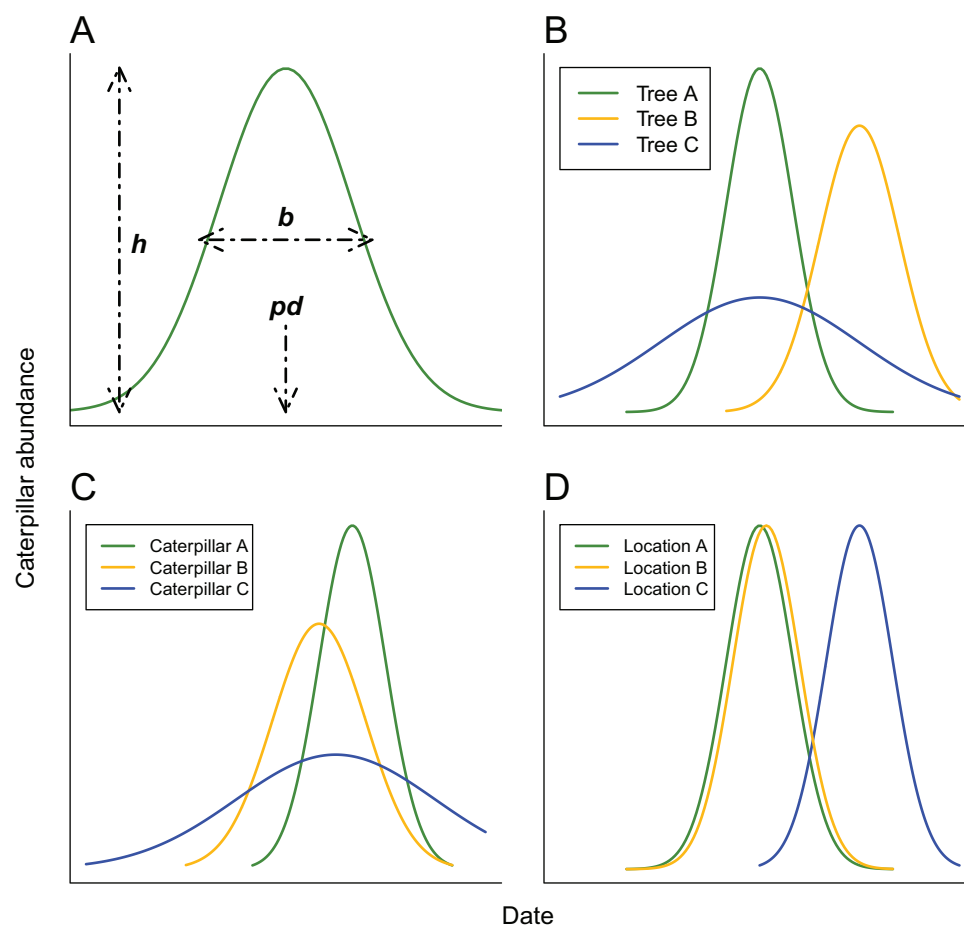


Figure 1: Schematic of potential temporal distributions of arboreal caterpillar biomass peaks in spring. A, Parameters of caterpillar temporal distribution that could vary. Abbreviations: pd = peak date; h = height of the peak; b = breadth (duration) of the peak (50% of total peak). B–D, Different contributions to variation in caterpillar temporal distributions. B, Tree species buffering hypothesis: how different tree taxa may have different caterpillar temporal distributions, with tree B showing a later peak than trees A and C and tree C having a lower, longer peak than trees A and B. C, Dietary buffering hypothesis: how different caterpillar species may show different spring peaks even on the same tree, with caterpillar A having the highest peak and caterpillar C having the longest. D, Landscape buffering hypothesis: how geographical locations could have differently timed spring caterpillar peaks, with locations A and B sharing a similar peak date and location C having a later peak date.

synchrony of winter moth larval hatching with host leaf bud burst is important for growth and survival (Feeny 1970; Buse and Good 1996; van Asch et al. 2007), and the same has been found for some other spring-feeding caterpillar species (Klemola et al. 2003; van Asch and Visser 2007). Leafing phenology of deciduous temperate tree species responds to spring temperature (Polgar and Primack 2011; Roberts et al. 2015), and winter moths and other caterpillars are able to synchronize well with host plants, likely by responding to similar temperature cues (Buse and Good 1996), as caterpillar phenology is largely determined by temperature (Buse et al. 1999; van Asch et al. 2012). Other locally abundant caterpillar species (such as green oak tortrix [*Tortrix viridana*]) may also be important to birds, and together these two caterpillar species were estimated to comprise ca. 75% of the spring caterpillar peak in an oak woodland in southern England (Hunter 1990, 1992), while winter moth alone were responsible for more than 80% of the peak in a primeval Polish forest during an outbreak year (Wesolowski and Rowinski 2006). However, because most studies on caterpillars have taken place in oak-dominated woodland, little is known about how the species composition of caterpillar communities varies among woodland habitats or whether winter moth is equally dominant.

The overall abundance and temporal distribution of arboreal caterpillars may also differ between tree species. In the United Kingdom, oak and willow (*Salix* sp.) harbor the highest diversities of caterpillar species, followed by birch (*Betula* sp.; Kennedy and Southwood 1984). It is unknown, however, whether tree species that host greater caterpillar diversities also host higher caterpillar abundances. The timing of the caterpillar peak may also vary between tree taxa, as with deciduous trees having an earlier and higher caterpillar peak than coniferous trees (Veen et al. 2010; Burger et al. 2012). However, among the native species of a genus (e.g., *Quercus*) in the United Kingdom, the temporal distribution of the caterpillar peak appears similar (Southwood et al. 2004).

The thermal environment can have a profound effect on ectotherms and varies substantially in space, generally getting colder with increasing elevation and latitude. Temperature is thought to act as a constraint on the latitudinal and elevational distribution limits of many Lepidoptera (Parmesan et al. 1999; Bale et al. 2002), manifested by a tendency for lower body mass and survival of caterpillars at the upper extremes of a species' elevational distribution (Alonso 1999; Hodkinson 2005). Increasing elevation might therefore reduce the height of the caterpillar biomass peak. Alternatively, because predation of caterpillars can be higher at lower elevations and latitudes (Roslin et al. 2017), this may allow for more frequent outbreaks of caterpillars at higher elevations (Raymond et al. 2002) and give rise to the opposite tendency. Colder conditions also retard phenology and

developmental rates of Lepidopteran larvae (Buse et al. 1999; Bale et al. 2002; Hodkinson 2005). This is seen in the timing of the caterpillar biomass peak, which is delayed by approximately 1.3 days for each degree of latitude northward in UK oak woodlands (Smith et al. 2011; Burgess et al. 2018). The timing of the caterpillar peak is also likely to delay with increasing elevation, as reported for adult Lepidopteran flight times (Gutiérrez and Menéndez 1998; Illán et al. 2012). Taken together, such processes could impact the temporal distribution of spring caterpillar peaks across elevational and latitudinal gradients and generate geographic variation in the shape and timing of the caterpillar peak (fig. 1D).

Here we sample caterpillars across 40 sites and 220 km (Shutt et al. 2018), identifying species via the cytochrome oxidase subunit I (COI) genetic barcode. We address three major aims to understand how the caterpillar community (and its phenological distribution) varies across space and tree species. First, we identify the species composition of the spring caterpillar community and the contribution made by dominant species, such as winter moth. Second, we estimate the effects of tree species, habitat, latitude, and elevation on the presence of (1) all caterpillars, (2) winter moths, and (3) the proportion of the caterpillar community that winter moths comprise. Finally, we focus on the temporal distribution of caterpillars and estimate how the timing, breadth, and height of the caterpillar peak varies among abundant tree species and with elevation (the major determinant of geographic variation in temperature in our study system). Addressing these aims provides insight into the factors that contribute to variation in the timing and height of the caterpillar peak, which may serve to buffer avian consumers from the effects of phenological mismatch.

Methods

Study System

This study was conducted along a 220-km transect of Scotland incorporating 40 woodland field sites (Shutt et al. 2018). All dates reported, unless explicitly indicated otherwise, are ordinal dates. The location of each nest box was determined using a handheld global positioning system (Garmin eTrex High Sensitivity) and elevation obtained (m asl) via the Google Maps elevation application programming interface. Habitat surveys were conducted at each of the field sites as detailed by Shutt et al. (2018), and spring tree phenology (first bud burst [FBB]) was studied on six to 10 individual focal trees per study site in each year. The number of study sites was 30 in 2014, 35 in 2015, and 37 in 2016, with 40 total sites (for details, see Shutt et al. 2018). Each focal tree was identified at the genus level, as were all trees included in the habitat survey, and the tree taxa studied represent all of the frequent deciduous tree species in the study area (Shutt et al. 2018).

Caterpillar Sampling

Branch beating was initiated at all study sites the day immediately after a threshold of 45% of focal trees along the entire transect were at or beyond the first leaf stage of their phenology in that given year and continuing until the end of the field season in each year (2014 sampling days 120–166; 2015 days 125–175; 2016 days 130–173). This aimed to sample phytophagous invertebrates from as early in the spring as possible while minimizing damage to underdeveloped buds and leaves on focal trees. Branch beating trees were selected at random from the pool of focal trees at each site, subject to the constraint that the tree had at least one branch with a minimum length of 1 m between 0.5 and 1.5 m above the ground. A suitable branch within reach on each selected focal tree was selected at random, identified, and maintained as the beaten branch for that focal tree, except in a limited number of cases where the branch broke or died. In 2014, three focal trees were sampled per site, with two focal trees beaten on the first visit and a different focal tree the next visit (2 days later), returning to the first two the visit after and continuing in that pattern until the conclusion of the field season, such that each branch was beaten every 4 days to allow caterpillar recolonization. In 2015 and 2016, the sampled branches were increased to six per site (four branches on the first visit and two on the second). While we cannot exclude the possibility that beating and collecting caterpillars from the same branch will bias the peak toward earlier dates by removing early-instar caterpillars and not letting them grow and add volume to the peak at a later date, the method was applied consistently across all sites and years.

Beating was done into a clear plastic rubble sack (76 cm × 51 cm) fully extended over the branch and foliage by holding the open end closed and facing upward and then beating the bag by hand 30 times at regular intervals and strength (about two per second) to dislodge invertebrates on the branch into the bag. After 30 beats, everything within the bag was counted. All caterpillars (invertebrate larvae appearing like those of *Lepidoptera* sp.) with an estimated diameter ≥ 1 mm were counted and collected by the beater (threshold chosen because smaller caterpillars are easy to overlook and provide very little resource to birds). Collected caterpillars were stored in pure ethanol and placed in a freezer. Weather was recorded in three categories (dry/wet/rain) along with the beater's identity.

Caterpillar Identification

The maximum length and width (mm) of stored caterpillars was measured to calculate volume, excluding samples that had become desiccated and thus no longer resembled their original proportions. A small portion of each caterpillar was removed with a sterilized scalpel. Polymerase chain reac-

tion and barcoding of 380 nondesiccated samples at the cytochrome c oxidase subunit I locus (640 bp) was conducted by the Biodiversity of Life Database (BOLD) in Guelph, Canada (Ratnasingham and Hebert 2007). Each caterpillar was photographed, and data can be accessed through the BOLD project BLUTI (<https://doi.org/10.5883/DS-PHEN1416>). A total of 317 samples were fully barcode compliant by having two complete sequences (forward and reverse), and an additional 44 had one complete sequence. All 361 of these samples were queried against BOLD and GenBank databases, with the best hit accepted, all to the species level. Of the 19 samples that failed to record a full sequence, 11 were assigned to the species level on the basis of the following criteria: the best hit had $>85\%$ identity match identical, including unread bases (N), and $>98\%$ when unread bases were ignored; the species was already known to occur on the transect through a successful barcode; and the best hit species was $>2\%$ better than the next best hit species. Incomplete barcodes that did not meet these criteria were recorded as unidentified ($n = 8$). Where more than one visually identical caterpillar was collected from the same branch on the same date, one was sent to BOLD and the other(s) assumed to be of the same taxon, and the individual was recorded as visually rather than genetically identified ($n = 105$). Species richness pools were estimated via the Chao equation (Chao 1987) implemented in the R package *vegan* (Oksanen et al. 2010).

Statistical Analyses

Caterpillar number per beating was converted into presence/absence for analysis. While this discards some information, there were insufficient cases ($n = 78$, 1.2% of beatings) where more than one caterpillar was sampled to run hurdle or zero-inflated Poisson models. To assess whether caterpillars are more frequently found where their host food plant is more abundant, we calculated local tree resource availability as the percentage of trees at the site that were of the same genus as the sampled tree.

A Bayesian generalized linear mixed model (GLMM) in the MCMCglmm R package (Hadfield 2010) was used to analyze how the probability of finding a caterpillar via branch beating varies across host tree taxa and biogeography (latitude and elevation). Caterpillar presence/absence in a beating sample was the response variable, with site mean latitude ($^{\circ}$ N), site mean elevation (m), year, and local tree availability as fixed effects and tree taxon sampled, site, individual tree identification (ID), date within year, and recorder ID as random effects, with a binomial error structure (logit link function). The effect of individual tree taxa was inferred on the basis of each species' random effect. We present full models (which we did not seek to simplify) and judge significance on the basis of credible intervals for fixed effects not overlapping

0. The same model structure as above was applied in two separate models to examine the predictors of (1) presence/absence of winter moth caterpillars and (2) the proportion of all caterpillars that winter moths comprise, although this last model differed slightly, as detailed in the appendix (available online).

To assess the effect of elevation on the temporal distribution of the caterpillar peak—omitting any effect of tree taxon—a GLMM was used with caterpillar presence/absence in a beating sample as the response, with date, date², elevation, and year with interactions between elevation and date and between elevation and date² included as fixed effects and site and tree ID as random effects, with a categorical error structure. From this model, we obtained elevation-specific predictions of peak ordinal date (the date on which the likelihood of finding a caterpillar was predicted to be at its highest), height of peak (the probability of finding a caterpillar on the peak date), and breadth of peak (length of time on either side of peak date, where the probability of finding a caterpillar is $\geq 50\%$ of the probability at the height of the peak). A nominate 50% of maximum height was used to quantify peak breadth, although the exact cutoff is not important for breadth comparisons because the breadths are based on the quadratic curve such that if a different cutoff were selected, the breadths would be perfectly correlated with those used.

To assess how tree taxa differ in the length of time between bud burst and reaching a caterpillar peak and how they affect the temporal distribution and shape of the caterpillar peak, the data set was reduced to samples from the four tree taxa that yielded >50 caterpillars: birch (*Betula pendula* and *Betula pubescens*), oak (*Quercus robur* and *Quercus petraea*), sycamore (*Acer pseudoplatanus*), and willow (*Salix* sp.). For each individual tree in each individual year, the time since FBB for each sampling date was calculated. A GLMM with presence/absence of caterpillars (across all years) as the response was constructed, with time since FBB, time since FBB², tree taxon, and year with interactions between tree taxon and time since FBB and FBB² fitted as fixed effects. The random effects were site and tree ID.

To project the temporal trends in caterpillar temporal distributions on the four tree taxa in terms of ordinal date rather than time after FBB, we considered a single site (STY; mean 56.48°N, −3.47°E; see Shutt et al. 2018), which was the only site with at least one FBB date recorded for each of the four focal tree species in every year. The mean FBB of each tree species across years was calculated and this date added to time since FBB to derive a prediction of the caterpillar temporal distribution across ordinal dates.

To test whether the temporal distribution of caterpillar biomass departs from the temporal distribution of caterpillar presence/absence, we reduced the data set further (within the four best estimated tree taxa as above) to include only successful beatings with measured caterpillars, and an estimated

volume (termed biomass for this study) of each caterpillar was calculated on the basis of πr^2 , where r is the radius. A GLMM similar to the one detailed above for assessing the presence/absence of caterpillars was then used to analyze this, with the response being log-transformed caterpillar biomass rather than presence/absence, using a Gaussian error structure rather than binomial. We then calculated predicted values for biomass of caterpillars on specific tree species across days since FBB by multiplying the posterior distribution of predicted values from the biomass and presence/absence models.

All GLMMs were run with sufficient iterations to provide good effective sample sizes ($n > 1,000$) for all the focal parameters; autocorrelation was ensured to be low, and convergence was inferred by visual inspection of trace plots. Numeric predictor variables (including dates and timings) were mean centered (Schielzeth 2010). Parameter-expanded priors were used for all models, with fixed residual variance (0.5) for categorical error structure models. A Bayesian equivalent of a two-tailed P value is calculated by determining the proportion of the posterior distribution that is less than or greater than 0 and multiplying the smaller of these values by 2. All analyses were conducted in R version 3.1.1 (R Development Core Team 2014). Data have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.71568mt>; Shutt et al. 2019).

Results

Caterpillars Sampled

A total of 575 caterpillars were collected over the course of the study and 477 identified to the species level (see “Methods”) from 6,320 branch beatings, comprising 62 species. Total transect-wide estimated species richness was 97 species (figs. 2, A1; figs. A1–A6 are available online). Some larvae were not *Lepidoptera* but were visually similar and included for analyses because they contribute to insectivorous bird diet and have been retained by some previous studies (Betts 1955; Marciniak et al. 2007). The 477 identified caterpillars included 445 *Lepidoptera* larvae (93.3%) of 45 species, 15 *Hymenoptera* larvae (3.1%) of 13 species, 11 *Diptera* larvae (2.3%) of three species, and six *Coleoptera* larvae (1.3%) of one species. Within the *Lepidoptera*, the most important constituent families were the *Geometrids* (347 individuals [78% of *Lepidoptera*] of 21 species) and the *Noctuids* (56 individuals [13% of *Lepidoptera*] of 10 species). Most species were rarely sampled, with only eight species comprising 15 or more identified individuals (winter moth *Operophtera brumata*: 156; scarce umber *Agriopis aurantiaria*: 67; northern winter moth *Operophtera fagata*: 27; variable smudge *Ypsolopha ustella*: 19; mottled umber *Erannis defoliaria*: 17; dotted border *Agriopis marginaria*: 16; common quaker *Orthosia*

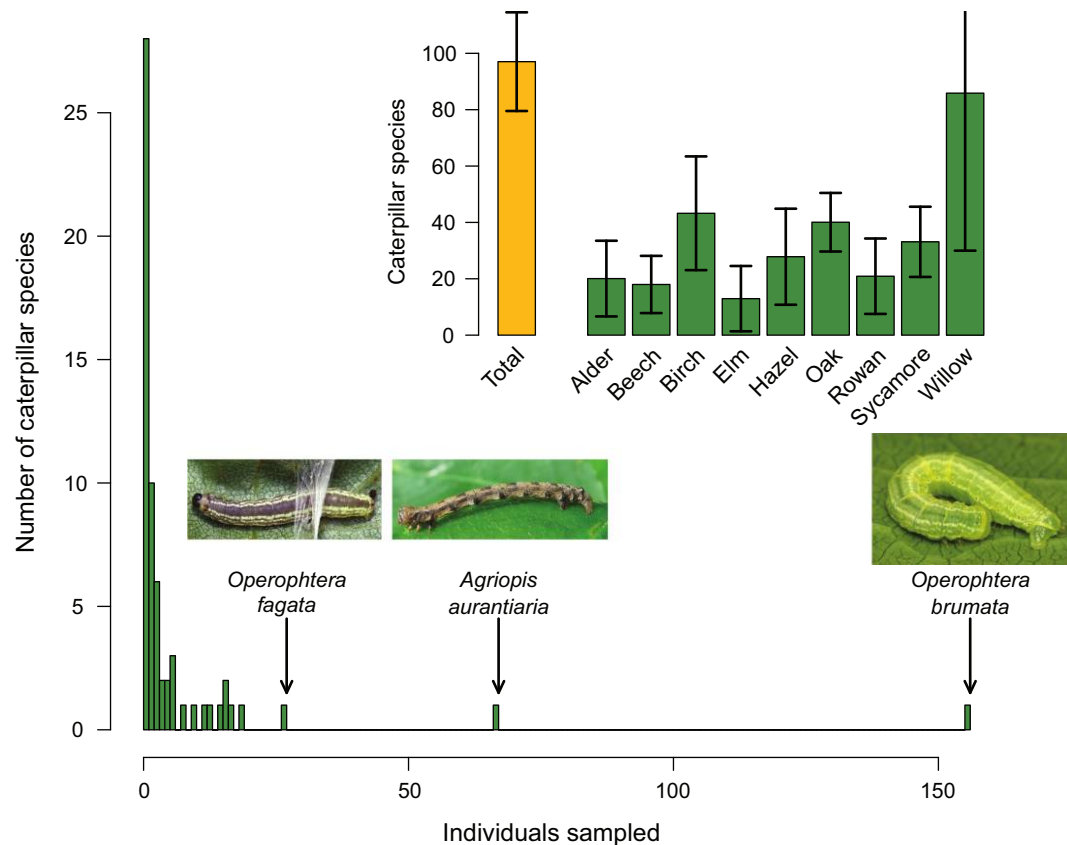


Figure 2: Histogram of number of individuals sampled of each species. *Inset*, estimated caterpillar species richness (\pm SE) accounting for sampling effort associated with tree taxa in this study (see “Methods”) and estimated caterpillar species richness of the transect as a whole (total). Tree taxa branch beaten but not included (ash, aspen, cherry, chestnut, and lime) yielded fewer than five caterpillar species; thus, their species richness pool could not be estimated. Tree taxa and constituent species are detailed in Shutt et al. (2018). Image credits (from left to right): Patrick Clement (CC-BY 2.0), Wouter Bosgra (CC-BY 3.0), and Donald Hobern (CC-BY 2.0).

cerasi: 16; chestnut *Conistra vaccinii*: 15), and the three most commonly sampled species comprised more than 50% of total caterpillars identified (fig. 2). For the sample size, host tree identities, and site presence for each caterpillar species, see table A1 (tables A1–A5 are available online).

There was clear evidence that species richness varied among tree taxa, being highest on oak ($n = 26$) through direct observation in this study (fig. A2) but predicted to be highest on willow ($n = 85$) once sampling effort is accounted for, although the willow prediction has a large associated error (fig. 2, *inset*). Latitudinal and elevational trends in the presence and abundance of the eight most commonly sampled species are reported in figures A3 and A4. Winter moth was sampled at almost every site (table A1). The next most common species (scarce umber and northern winter moth) favor birch-dominated sites, with scarce umber being more numerous at higher elevations (table A1; fig. A4).

Tree Taxon and Biogeographic Effects on Caterpillar Presence

The probability of sampling a caterpillar showed no significant latitudinal or elevational trend, nor was there a significant effect of the amount of host tree taxon locally available (table A2). Caterpillars were sampled at a significantly higher rate overall in 2014 than in 2015 or 2016. The probability of sampling a caterpillar varied significantly among tree taxa, and the variation among dates within a year is of similar magnitude. Among-site variation and the effect of individual tree ID is much less pronounced, and the effect of recorder was poorly estimated, with a large associated error.

For winter moths, interannual differences were less pronounced and nonsignificant, and there remains no trend in the probability of occurrence with latitude or elevation (table A2). However, the availability of host tree taxon

significantly predicts occurrence, with rarer tree taxa in the local environment having a greater probability of sampling a winter moth caterpillar. The probability of sampling a winter moth varied significantly among dates within a year, with variance between tree taxa of a similar magnitude but with a broader posterior (i.e., greater uncertainty). Variance among sites was slightly lower. Winter moths were an equally important component of the total spring caterpillar peak across all tree taxa, with no significant difference in the proportion of winter moths within the total caterpillar peak between tree taxa (appendix; fig. A5).

The 95% credible intervals (CIs) derived from the random effects for each tree taxon revealed a significantly greater probability of sampling a caterpillar on oak and willow than the average tree taxon, with the same being true of winter moth caterpillars (fig. 3). While the random effects for the other tree taxa do not deviate significantly from zero, the median random effect for birch is positive, whereas for alder and ash this is negative, suggesting that these taxa were the least likely to host a caterpillar in spring among the tree taxa studied, with alder and rowan being the least likely to host a winter moth caterpillar (fig. 3).

Tree Taxon and Elevation Effects on the Temporal Distribution of the Spring Caterpillar Peak

After FBB, there was a general tendency for a quadratic humped relationship of caterpillar presence over time (table A3). The linear and quadratic slopes for oak were significantly steeper than those for birch, but the coefficients for sycamore and willow did not depart significantly from

those estimated for birch. Comparing the predicted temporal distributions of caterpillar peaks among tree taxa, we can identify how the timing of the peak relative to bud burst, height, and width varies. Compared with birch, oak shows a higher but shorter peak sooner after FBB; sycamore shows a lower, shorter peak sooner after FBB; and willow shows a higher, longer peak later after FBB (figs. 4, 5). The caterpillar peak on willow was significantly more delayed after FBB than for oak, and oak and willow had significantly higher caterpillar peaks than sycamore. When these timings were converted to ordinal dates, the difference in timing is reduced such that the caterpillar peaks on all trees are approximately synchronous (fig. 5B).

Focusing on caterpillar biomass rather than probability of occurrence, the temporal distribution is not humped but continues exponentially to the end of the study period (table A3). Multiplying the posterior distributions of the predictions for occurrence and biomass together reveals that the actual peak in caterpillar biomass available in the spring is later (ca. 10 days) for all analyzed tree taxa than when only caterpillar occurrence is considered (fig. 5A). Because this differs slightly between tree taxa, it also gives rise to a more synchronous peak between birch, sycamore, and oak (fig. 5B), with mean peak dates within 10 days of each other (birch: 170.5; oak: 172.3; sycamore: 162.9) and substantial overlap in CIs. The heights and breadths of the caterpillar biomass peak do not differ between taxa (fig. 5C, 5D). Willow is estimated too poorly by the biomass model to be analyzable because of its late occurrence peak resulting in a wide variance in predicted peak dates, which extend long after the end of our sampling period.

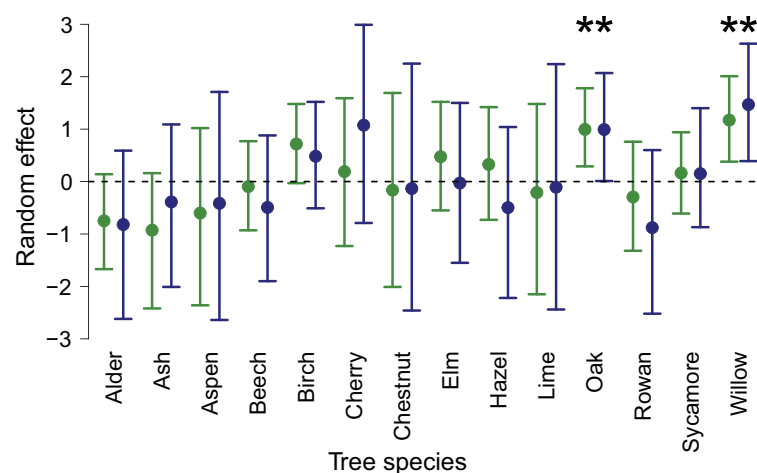


Figure 3: Posterior median and 95% credible intervals of random effects (can be interpreted as deviations in the probability of finding a caterpillar) for each tree taxon when analyzed as a random effect in the generalized linear mixed models described in table A2 (available online). Green lines = full caterpillar model; blue lines = winter moth model. Credible intervals that do not cross zero correspond to random effects that depart significantly from the mean effect, and asterisks indicate significant results.

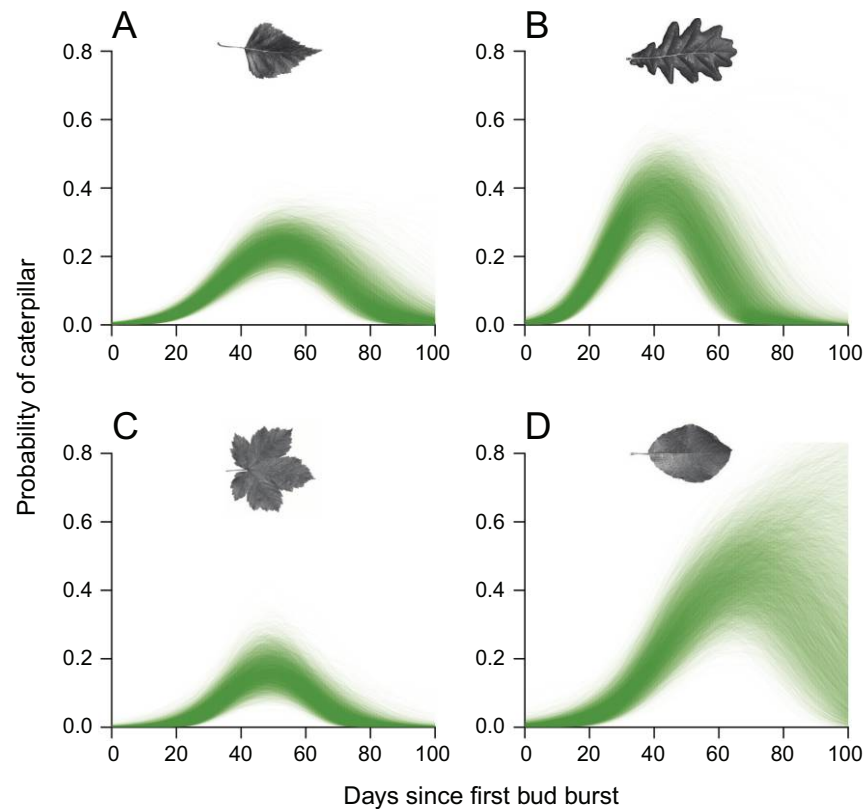


Figure 4: Probability of caterpillar occurrence on days after first bud burst for birch (A), oak (B), sycamore (C), and willow (D). Posterior distributions from a generalized linear mixed model (reported in table A3 [available online]) for 2014 are depicted, with all other variables at their mean.

When the effects of tree taxa were excluded, the effect of elevation on the temporal distribution of the spring caterpillar peak becomes pronounced (table A4). There is a humped relationship between timing and the probability of caterpillar occurrence (table A4). In addition, there was a significant interaction between date and elevation, such that increasing elevation delayed the peak date of caterpillars. Comparing predictions at low (sea level) and high (450 m asl) elevations, we found a significantly earlier (-16.7 days, 95% CI: -36.9 to -4.5) and lower (-0.31 , 95% CI: -0.60 to -0.05) peak at sea level (figs. 6, A6). However, the breadth of the peak was not significantly different between low and high elevations (95% CI: -34.7 to 17.3 ; median: -2.5). Note that the predictions at sea level are substantially more tightly estimated (fig. 6).

Discussion

This study identifies a diverse arboreal spring caterpillar peak dominated by a small number of species, in accordance with previous studies (Hunter 1992; Butler and Strazanac 2000; Wesolowski and Rowinski 2006), with winter moth accounting for one-third of all caterpillars identified and

the three commonest species accounted for more than half of all caterpillars collected. Host tree taxon has a large effect on the availability of caterpillars in spring, including generalist winter moths, with oak and willow being the only two tree taxa significantly more likely to have a caterpillar sampled from them than the average tree taxon. While biogeography had little effect on the probability of caterpillar or winter moth occurrence, it had pronounced effects on the temporal distribution of caterpillars, with peak date delayed by 3.7 days per 100-m increase in elevation and the height of the peak increasing with elevation. While the timing delay may be attributable to the lapse rate of temperature with elevation, the increase in peak height may arise via an increase in the amount of willow at the higher elevation sites (Shutt et al. 2018). This study therefore provides evidence that the temporal distribution of caterpillars is geographically variable because of environmental heterogeneity.

Caterpillar diversity is known to vary among host tree species, being higher on native and more abundant tree species in the landscape (Southwood 1961; Fuentes-Montemayor et al. 2012). Such diversity in host tree quality for supporting caterpillars was corroborated by this study, but we address the question across a much larger range of native and

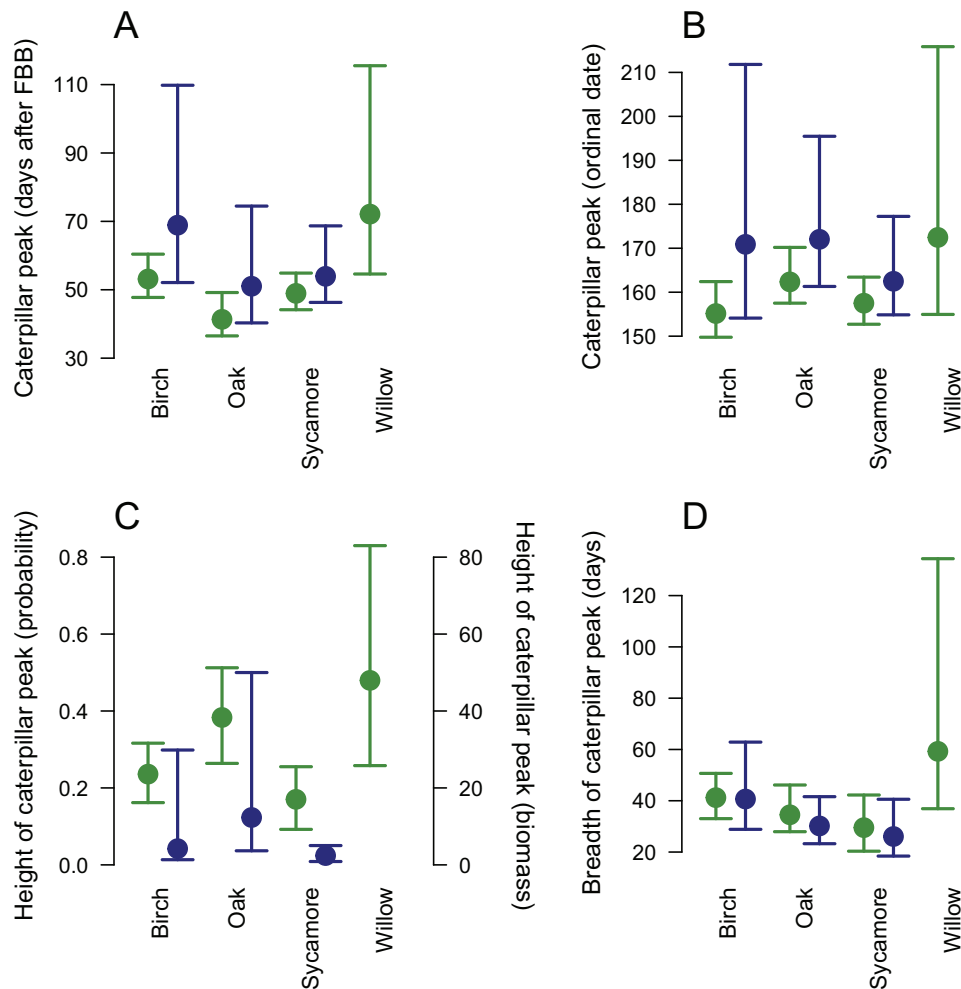


Figure 5: Means and 95% credible intervals for timing of peak (days after first bud burst [FBB]; A), timing of peak (ordinal date; B), height of caterpillar peak (probability of caterpillar occurrence for probability, biomass peak for biomass; C), and breadth of caterpillar peak (days; D) across four tree taxa. Predictions derived from the two posterior distributions from generalized linear mixed models (reported in table A3 [available online]) for 2014 are depicted, with all other variables at their mean. Green lines = probability results; blue lines = biomass results.

widespread broadleaf trees than previously considered and extend it to include the variance in the temporal distribution of caterpillars in relation to the spring peak for the most common tree taxa. Oak and willow have previously been identified as hosting the highest caterpillar diversities in the United Kingdom (Kennedy and Southwood 1984; Waring and Townsend 2017), and this study extends this to show that these taxa also have the highest caterpillar abundance and spring peaks. However, the time from bud burst to peak was later for willow and lasted longer, which may be the result of a longer period of leaf palatability compared with oak. The palatability of both oak (Feeny 1970; van Asch and Visser 2007) and willow (Kirsten and Topp 1991; Ruuhola et al. 2001) for caterpillars declines over the season because of reduced nutritional content of leaves and a buildup in de-

fensive chemicals, but these results may suggest that these defensive chemicals either are less effective against common caterpillar species or take longer to accumulate in willow.

Winter moths were detected on almost all tree taxa sampled, with oak and willow hosting higher abundances, supporting previous work that indicates that while this species is a generalist feeder, they do show some host tree preference (Wesolowski and Rowinski 2006). Winter moths also seemed to outbreak more on willow at higher elevations (fig. A3; J. D. Shutt, personal observation) along the transect, agreeing with previous research suggesting that outbreaks are more likely to occur at higher elevations (Raymond et al. 2002) possibly because of lower predation and parasitism. Winter moths were also significantly more likely to occur on less abundant host plants within the local environment,

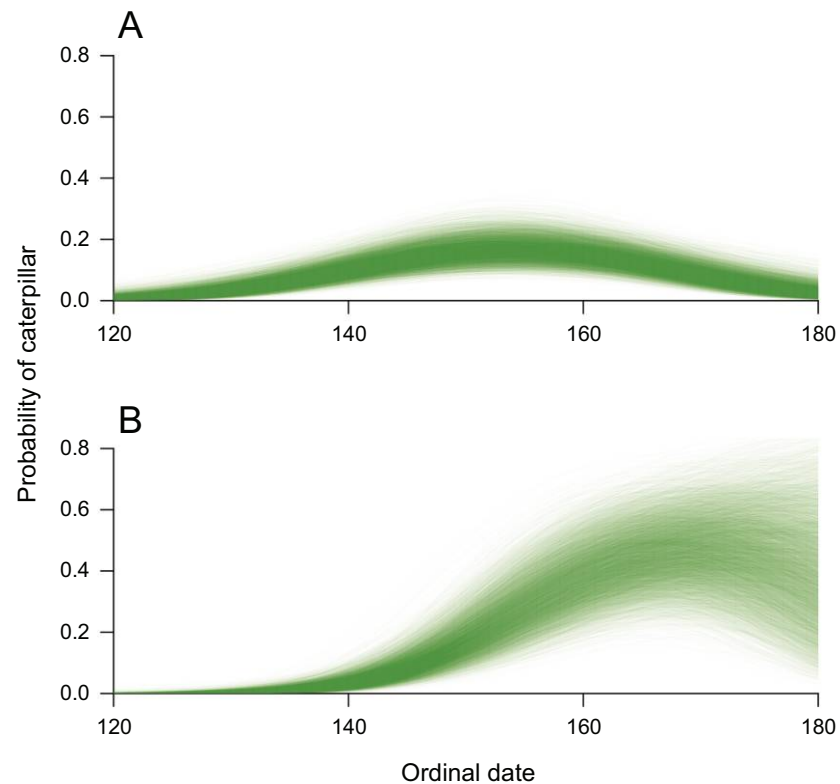


Figure 6: Predicted probability of finding a caterpillar via branch beating throughout spring (ordinal date) at sea level (A) and at 450 m asl (B). Elevations are roughly equivalent to the lowest and highest points along the transect (Shutt et al. 2018). Posterior distributions from a generalized linear mixed model (reported in table A4 [available online]) for 2014 are depicted, with all other variables at their mean.

contradicting the general consensus that caterpillars are more frequent on locally common species (Kelly and Southwood 1999; Wesolowski and Rowinski 2006). This is also likely due to the outbreak tendency on willow at high elevations, where willow is not the commonest local tree taxon (Shutt et al. 2018) and frequently oak was also not the commonest local tree taxon. The broadly temporally coincident caterpillar peaks across tree taxa with respect to ordinal date (rather than time since bud burst of a given tree) could also give credence to the idea that winter moth caterpillar emergence is locally adapted to the most important host tree in a given landscape and feed on other tree species opportunistically (Kirsten and Topp 1991; Wesolowski and Rowinski 2006). Another possibility is that winter moths are adapted to an average phenology of multiple host trees.

Biogeography was found to have little effect on caterpillar presence, with neither latitude nor elevation having a significant effect, running contrary to previous studies that found decreases in caterpillar abundance with increasing elevation and latitude (Garibaldi et al. 2011; Smith et al. 2011; Pellissier et al. 2012), possibly because our study was conducted on a smaller spatial scale. Elevation did, however, significantly

affect the temporal distribution of caterpillars, with the peak date delayed by 3.7 days per 100-m rise in elevation. Previous studies have shown a delay in caterpillar emergence in response to increasing elevation (Smith et al. 2011), but this is the first study as far as we are aware to estimate the change in date of the spring caterpillar peak over an elevational gradient. The delay in caterpillar peak date with increasing elevation is probably due to lower temperatures delaying hatching and growth (Buse et al. 1999; Bale et al. 2002), with the mean March/April temperature difference between our lowest and highest sites being 3°C while the latitudinal temperature difference along the transect is negligible.

The caterpillar peak date was delayed by ca. 10 days when the biomass (volume) of caterpillars was factored in addition to likelihood of occurrence. This was due to caterpillar volume increasing throughout the study period while probability of occurrence followed a parabola, as in previous studies (Naef-Daenzer and Keller 1999). Both the temporal distribution of caterpillar occurrence and the size of the caterpillars available are important for passerine predators (Naef-Daenzer and Keller 1999; Naef-Daenzer et al. 2000), and the product of these two measures should estimate the

true peak of total caterpillar biomass that is most relevant to insectivorous woodland passerine resource availability (Visser et al. 1998; Charmantier et al. 2008).

Our findings have implications for understanding how far insights into the match/mismatch hypothesis generalize. We find that winter moths are easily the most abundant of the spring caterpillar species across most habitats and locations, supporting a general expectation that this species is a key component in the food chain (Visser et al. 1998; Wesolowski and Rowinski 2006). We also find evidence to support the importance of oak at the base of the food chain but also evidence that willow is host to a similar high level of caterpillars (table A3; fig. 6) and a caterpillar peak of greater duration than in other tree taxa, which could mean that mismatch in willow-dominated habitats could have less severe consequences than mismatch in other habitats. Elevation also affected caterpillar peak date (fig. 4), generating geographic variation in peak date (Both et al. 2004; Smith et al. 2011; Burgess et al. 2018). The degree to which this elevational variation in peak resource gives rise to variation in mismatch will depend on the degree to which the breeding phenology of avian consumers can track this.

The degree to which our specific tree taxa findings can be directly generalized on a broader spatial scale is unknown. We did not, for example, detect the presence of green oak tortrix, a caterpillar species that has been found to be twice as common on oak as winter moth in Wytham Woods in southern England (Hunter 1990, 1992). If the degree of interspecific competition among caterpillars on a single tree is weak, the presence of green oak tortrix may lead to oak being an even richer source of caterpillar abundance in England than found here in Scotland. In addition, aspen did not register a single caterpillar, despite being previously noted as having high diversity and palatability (Kennedy and Southwood 1984; Schwartzberg et al. 2014). We think that this is primarily due to timing, as aspen is exceptionally late in developing its first spring leaves (at the very end of the sampling period) and has new growth throughout the summer, supporting higher caterpillar diversities in late summer than in early spring (Niemela and Haukioja 1982; Niemela et al. 1982). However, it is clear that caterpillar diversity and abundance varies with respect to geographic location, time, and host tree taxon and that all three of these factors interact to shape the local spring caterpillar peak.

The caterpillar sampling method that we applied—branch beating—allowed us to directly sample, measure, and identify the caterpillars on the foliage, providing advantages over other methodologies, such as frass fall and half fall, the limitations of which are discussed in the introduction. However, branch beating also presents some disadvantages. For example, by removing sampled caterpillars and resampling branches, we may alter the potential future sampling and peak biomass. We resampled every 4 days to allow time for

recolonization, but the effect of our sampling approach on the subsequent probability of sampling requires further testing. It is also likely that this approach undersamples leaf-rolling and leaf-tunnelling moths and species with a canopy preference. Finally, only a small number of beatings yield a caterpillar, requiring high replication in order to draw useful inferences regarding the temporal distribution.

Conducting this study along a 220-km transect incorporating 40 variable field sites allowed us to investigate the factors that influence the caterpillar resource peak over a much wider geographical area than previously. Our results suggest that the ability of local tree diversity to mediate the effects of trophic mismatch for the birds in this system (the tree species buffering hypothesis) may be limited, as while the height of the peak varies between tree taxa, the date of the peak is very similar across tree taxa (fig. 1B). This indicates that while certain tree taxa provide higher resource levels than others, the peak date of resources is synchronous across tree taxa. The mean predicted peak dates of the focal tree taxa are within 10 days of one another, with overlapping CIs, and this falls inside the within-site among-individual variation in blue tit breeding phenology in a typical year (Phillimore et al. 2016; Shutt 2018). Similarly, peak date did not vary significantly with latitude on this scale (as in locations A and B in fig. 1D), whereas increasing elevation did delay peak date (like location C in fig. 1D). This allows for the possibility of the landscape buffering hypothesis of trophic mismatch at a population scale via elevational gradients. The dominance of certain caterpillar species in forming the peak reduces the possibility of buffering by dietary change (the dietary buffering hypothesis), as synchrony with these few species will be paramount (fig. 1C). Taken together, these results illustrate spatial heterogeneity in the spring woodland caterpillar peak at a regional scale, which may have important implications for the mesoscale ecological implications of climate change-induced trophic mismatch.

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